Acknowledgements

The Foundation for Research Development and the University of Natal Research Fund are thanked for financial support.

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Pollen morphology of *Periploca* (Periplocaceae)

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Received 3 January 1994; revised 29 March 1994

The pollen morphology of all 13 species of *Periploca* L. was studied. All the species are characterized by pollen grains arranged in tetrads. The arrangement of the grains may be rhomboidal, decussate or linear. Linear tetrads were only observed in *P. acuminata* Rahman & Wilcock, *P. sepium* Bunge and *P. aphylla* Decaisne. The exine is smooth. Exine structure consists of an outer, homogenous stratum (tectum) subtended by a granular stratum. Except for small differences which may occur between species in pollen size, the pollen is uniform in morphology.

Die stuifmeelmorfologie van al 13 spesies van *Periploca* L. is bestudeer. Al die spesies word gekenmerk deur stuifmeelkorrels wat in tetrades gerangskik is. Die rangskikking van die stuifmeelkorrels kan romboïdaal, kruisgewys of lineêr wees. Lineêre tetrades is net in *P. acuminata* Rahman & Wilcock, *P. sepium* Bunge en *P. aphylla* Decaisne waargeneem. Die eksien is glad en bestaan uit 'n buitenste homogene stratum (tektum) en 'n granulêre stratum daaronder. Met die uitsondering van klein verskille tussen spesies in stuifmeelgrootte, stem die stuifmeelkorrels in morfologie ooreen.

Keywords: *Periploca*, Periplocaceae, pollen morphology.

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Introduction

The Periplocaceae and Asclepiadaceae are two closely allied families having several features in common. The former was a subfamily of the Asclepiadaceae, but was raised to family status by Schlechter (1924), a concept followed by Bullock (1957). In both Periplocaceae and Asclepiadaceae the fruit consists of paired or single follicles and seeds have comas of hairs. The Periplocaceae is commonly distinguished from the Asclepiadaceae on the basis of floral characters like translators (pollen carriers) and pollen grains united in tetrads in contrast with pollinia attached to wishbone-shaped caudicles in the Asclepiadaceae. Kunze (1993) described the problem of homology between the translators in Periplocaceae and Asclepiadaceae and elucidated the hypothesized evolution of the asclepiad translator from periplocoid ancestors. Dave and Kuriachen (1991) showed that fruit characteristics can also be used to distinguish the families. The air chambers found in the fruit wall of Asclepiadaceae are absent in Periplocaceae follicles. The sclerenchymatous endocarp of Periplocaceae is 3 – 20 layers thick, whereas that of Asclepiadaceae is 1 – 6 layers

thick.

The Periplocaceae is basically confined to the Old World, and is found in Africa, Madagascar, Asia and Australia, and also in southern Europe in the case of *Periploca*. The family comprises some 45 genera and 180 species. Approximately 22 of these genera and about 86 species occur in Africa. The genus *Periploca* L. was revised by Browicz in 1966. Since this taxonomic revision of *Periploca* in 1966 when eleven species were identified, a new species from Bangladesh, *P. acuminata* Rahman & Wilcock, was described (Rahman & Wilcock 1992). *Periploca brevicoronata* D.J. Goyder & L. Boulos, which was described as a new species from southwest Arabia (Goyder & Boulos 1990), was placed in synonomy with *P. somaliense* Browicz by Venter and Verhoeven (1993). A thirteenth member, *P. gracilis* Boiss. [= *Cyprinia gracilis* (Boiss.) Browicz in Browicz 1965] completes the complement of *Periploca* species. Browicz (1966) divided his eleven species into two sections: *Periploca* L. and *Immaculata* Browicz. Species included in section *Immaculata* are *P. calophylla* (Wight) Falconer, *P. hydaspidis* Falconer and *P. linearifolia* Quartin-Dillon et Richard. Section *Periploca* was subdivided into three series: *Connatae* Browicz (*P. graeca* L. and *P. sepium* Bunge); *Laevigatae* Browicz (*P. laevigata* Aiton, *P. chevalieri* Browicz, *P. angustifolia* Labill. and *P. somaliense* Browicz); and *Aphyllae* Browicz [*P. aphylla* Decaisne and *P. visciformis* (Vatke) Schumann]. *P. acuminata* and *P. gracilis* both belong to section *Immaculata* (Venter & Verhoeven, in prep.).

Periploca is distinguished as a genus by the structure of its flowers. The corolla tube is shallow with the gynostegium exposed, the corolla lobes are with or without adaxial white-spotted glandular centres and flap-like coronal segments, and the anthers are hairy. Most of the *Periploca* species are climbers or semi-climbers. A few are erect shrubs. The majority of *Periploca* species inhabit desert or semi-desert environments, while a few are found in mesic forests. They are limited to the Old World in their distribution, from the Cape Verde Islands and the Canary Islands to North China and from the Balken Peninsula to Malawi in East Africa (Browicz 1966).

This paper constitutes part of a comprehensive palynological investigation and taxonomic revision of the Periplocaceae currently being undertaken by the authors.

Material and Methods

Specimens examined

Periploca acuminata Rahman & Wilcock: Sylhet, Bangladesh, Sep. 1987, *Rahman & Hossain 56* (ABD).

P. angustifolia Labill.: Mogador, Morocco, Feb. 1931, *Trethwey 117A* (K); Sallum, Egypt, June 1961, *Batanoung 3* (K); Mgarr, Malta, Oct. 1974, *Westra & Van Rooden 246* (G).

P. aphylla Decaisne: Prov. Laghman, Afghanistan, Apr. 1970, *Podlech 17562* (K); Bebehan, Iran, Mar. 1974, *Davis & Bokhari D55731* (K); Muzaffarabad, Pakistan, Apr. 1976, *Mohammad 2326* (K).

P. calophylla (Wight) Falconer: Yunnan, China, Apr. 1924, *Forrest 25469* (K); Yunnan, China, no date, *Henry 9130* (K).

P. chevalieri Browicz: no locality, 1865, no collector (K).

P. gracilis Boiss. [= *Cyprinia gracilis* (Boiss.) Browicz]: Omodhos, Cyprus, May 1979, *Hewer 4650* (K); Troödos, Cyprus, June 1956, *Kennedy 1860* (K).

P. graeca L.: Hazi-Omran, Iraq, June 1948, *Chapman 11921* (K); Zawita, Iraq, no date, *Robertson 56* (K); Istanbul, Turkey, June 1894, *Herbier de Bertram v.d. Post s.n.* (G).

P. hydaspidis Falconer: Kashmir, India, Sep. 1920, *Stewart 6083* (K).

P. laevigata Aiton: Monte Lentiscal, Gran Canaria, Dec. 1966, *Kunkel 9637* (SRGH); Prisco de Oro, Tenerife, Nov. 1903, *Teneuiffe 51* (K).

P. linearifolia Quartin-Dillon et Richard: North Kinango Escarpment, Kenya, July 1962, *Williams EAH 12577* (K); Lushoto Township, Tanzania, June 1961, *Semsei 3235* (K); Shoa Prov., Ethiopia, Oct. 1969, *De Wilde 5818* (K).

P. sepium Bunge: Peking, China, May 1880, *Hancock 37* (K).

P. somaliense Browicz: Ibb, Yemen, Apr. 1976, *Wood 1041* (K); Biljushi, Saudi Arabia, Mar. 1980, *Collenette 1287* (K).

P. visciformis (Vatke) Schumann: Farada Pass, Yemen, Mar. 1980, *Wood 3168* (K); Salalah, Oman, Oct. 1977, *Radcliffe-Smith* 5390 (K).

Methods

Pollen was obtained from herbarium specimens from the following herbaria: ABD, G, K and SRGH. For light microscopy (LM), pollen was acetolysed according to the method of Erdtman (1960),

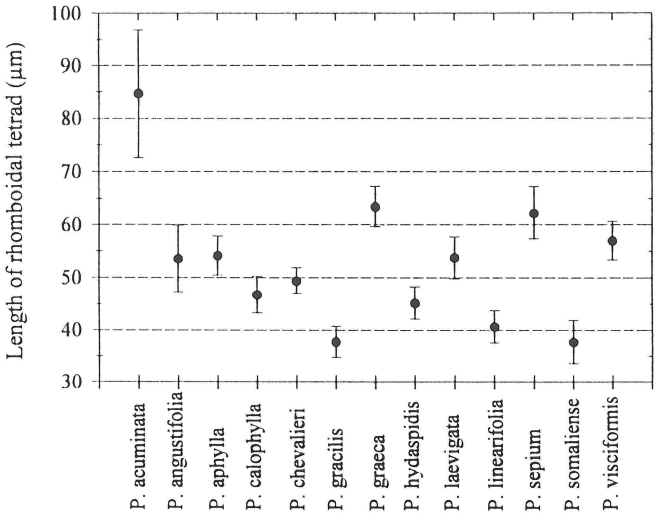
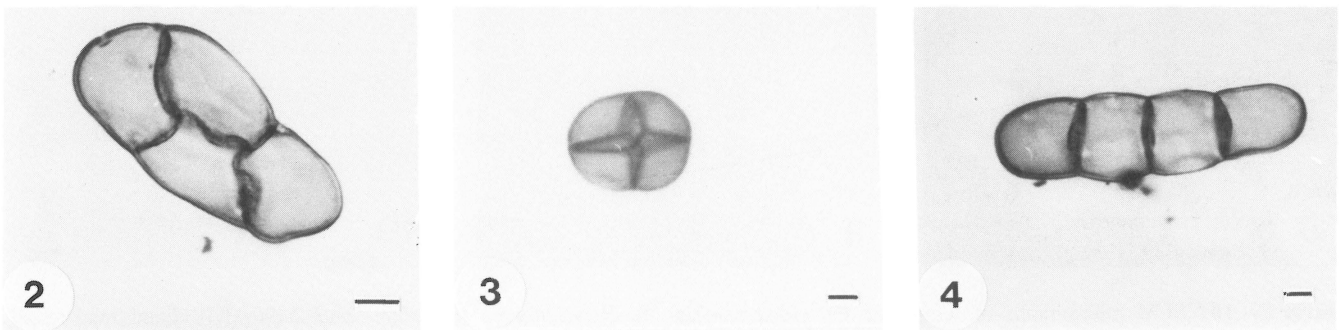


Figure 1 Length of rhomboidal tetrads of *Periploca* species. Mean value and standard deviation.



Figures 2 – 4 LM micrographs of tetrads of *Periploca* species. **2.** *P. graeca* [*Robertson 56* (K)] rhomboidal tetrad. **3.** *P. linearifolia* [*De Wilde 5818* (K)] decussate tetrad. **4.** *P. sepium* [*Hancock 37* (K)] linear tetrad. Scale bars: 10 µm.

mounted in glycerine jelly and sealed with paraffin wax. Samples were examined with a Zeiss photomicroscope. Measurements of tetrad size were, whenever possible, based on a minimum of 15 tetrads per specimen. For scanning electron microscopy (SEM), pollen was acetolysed, air-dried on stubs, coated with gold and examined with a Jeol Winsem 6400 microscope. For transmission electron microscopy (TEM), acetolysed pollen was fixed in 1% osmium tetroxide, stained with 0.5% uranyl acetate, dehydrated in ethyl alcohol and embedded in epoxy resin (Spurr 1969). Sections were cut with a glass knife, stained with uranyl acetate followed by lead citrate, and examined using a Philips 300 electron microscope at 60 kV.

Table 1 Diameter of pollen tetrads

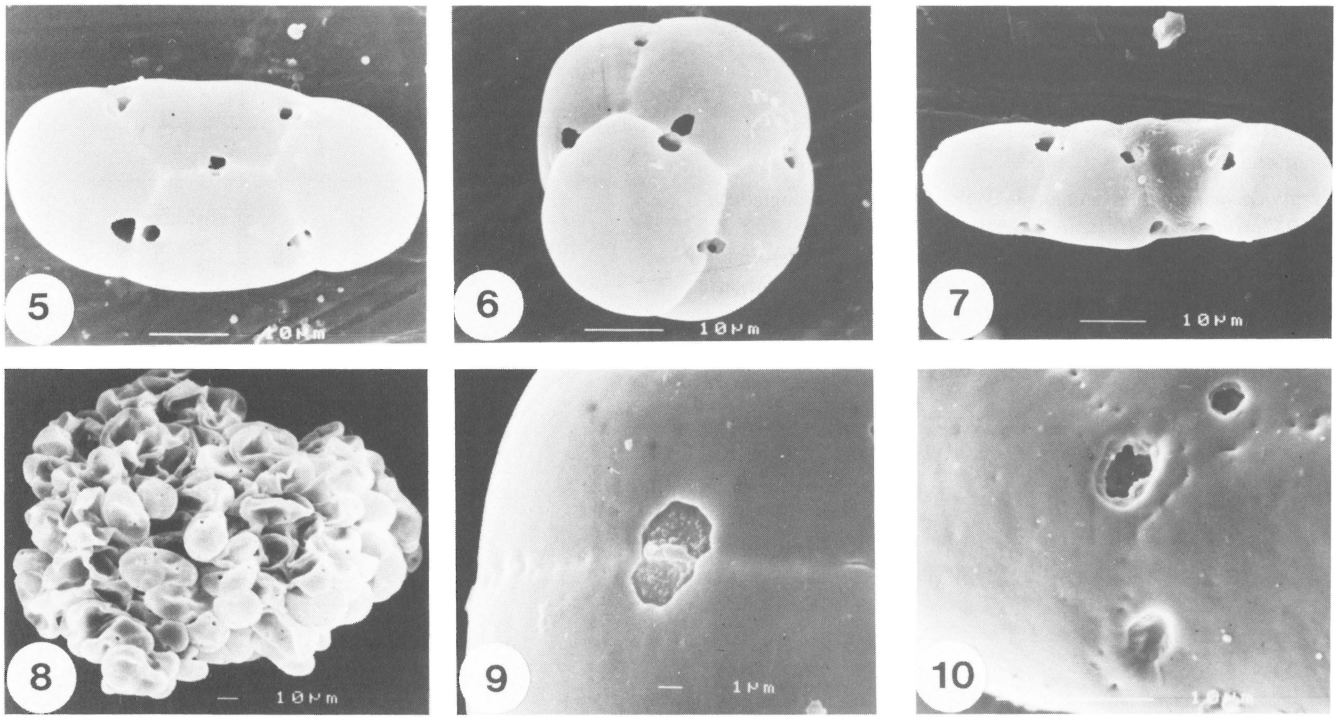
Taxon		Rhomboidal tetrad size (μm)
P. acuminata		84.7 (70 –108) ±12.1 × 42.8 (32 – 59) ± 8.6
P. angustifolia	1	50.5 (41 – 60) ± 5.3 × 27.7 (20 – 34) ± 3.2
	2	52.3 (45 – 59) ± 4.8 × 26.2 (22 – 29) ± 2
	3	58.7 (50 – 72) ± 4.9 × 28.9 (23 – 32) ± 2.3
P. aphylla	1	53.2 (45 – 61) ± 3.9 × 29.1 (23 – 33) ± 2.7
	2	55.3 (52 – 60) ± 2 × 27 (23 – 31) ± 1.7
	3	54.4 (44 – 65) ± 4.1 × 28.5 (23 – 32) ± 2.2
P. calophylla	1	47.8 (44 – 56) ± 3.6 × 28.7 (26 – 32) ± 1.7
	2	45.8 (40 – 51) ± 3.1 × 26.4 (23 – 31) ± 2
P. chevalieri		49.6 (45 – 55) ± 2.4 × 28.2 (24 – 32) ± 2
P. gracilis	1	38.4 (34 – 44) ± 3 × 27.7 (25 – 31) ± 1.8
	2	35.6 (34 – 37) ± 1 × 27.4 (25 – 30) ± 1.6
P. graeca	1	62.1 (57 – 68) ± 3.1 × 31.6 (28 – 39) ± 3.9
	2	64.4 (60 – 68) ± 3.5 × 33.3 (29 – 41) ± 3.1
	3	63.1 (56 – 74) ± 4.5 × 32.6 (29 – 41) ± 3.3
P. hydaspidis		45.3 (41 – 52) ± 3 × 27.6 (23 – 32) ± 2
P. laevigata	1	51.6 (44 – 61) ± 5.7 × 32.4 (27 – 37) ± 3.7
	2	53.9 (49 – 64) ± 3.8 × 27.5 (23 – 32) ± 2.5
P. linearifolia	1	39.4 (36 – 45) ± 3.5 × 28.6 (22 – 32) ± 3.2
	2	40.6 (36 – 47) ± 3.4 × 26.1 (23 – 30) ± 2.4
	3	41.6 (38 – 48) ± 2.4 × 25.8 (23 – 29) ± 1.8
P. sepium		62.3 (55 – 74) ± 4.9 × 31.2 (25 – 36) ± 2.8
P. somaliense	1	38.4 (29 – 45) ± 4.2 × 17.6 (15 – 21) ± 2.1
	2	34.5 × 19.5
P. visciformis	1	55.9 (50 – 65) ± 3.6 × 30.7 (25 – 35) ± 2.9
	2	58.4 (52 – 64) ± 3.4 × 37.4 (32 – 43) ± 3.6

Results

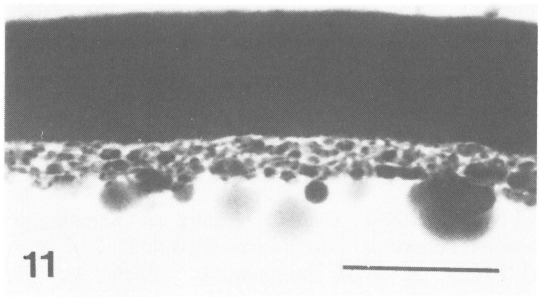
The pollen grains are united in calymmate tetrads with the grains arranged rhomboidally (Figures 2 & 5), decussately (Figures 3 & 6) or linearly (Figures 4 & 7). Linear grains were observed only in *P. sepium, P. acuminata* and *P. aphylla.* In the latter species they were observed very seldomly. Tetrads are often grouped together in *P. acuminata* and *P. laevigata* (Figure 8). Mean rhomboidal tetrad size for all pollen measured, ranged from 35 to 85 μm in length and 18 to 43 μm in width with an overall mean of 51.5 × 28.9 μm (Table 1, Figure 1). Pores 4 – 6, varying in size from 0.9 to 4.0 μm in diameter. Pores are sometimes covered with a thin layer of exine material (Figure 9). Inner pore edge is often uneven (Figure 10). Exine is smooth and stratified into a distal stratum (tectum), 0.3 – 0.55 μm thick, subtended by a granular stratum consisting of granules of unequal size, often fused to form a nearly continuous layer (Figures 11 – 13). The tectum and granular stratum are separated by a line where an osmiophilic substance is present (Figure 12). The inner side of the exine (granular stratum) gives the impression of a crust with irregular spaces and small protuberances (Figure 14). The inner walls separating the individual grains of the tetrad consist of two adjoining tectums each subtended by a granular stratum (Figure 15).

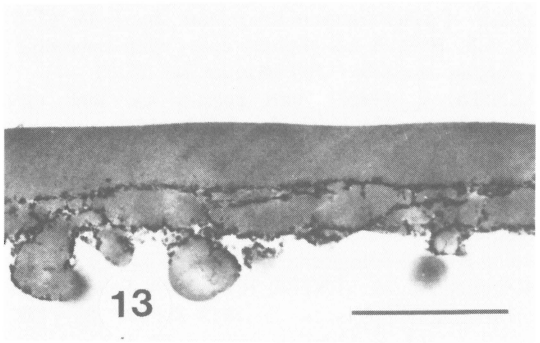
Discussion

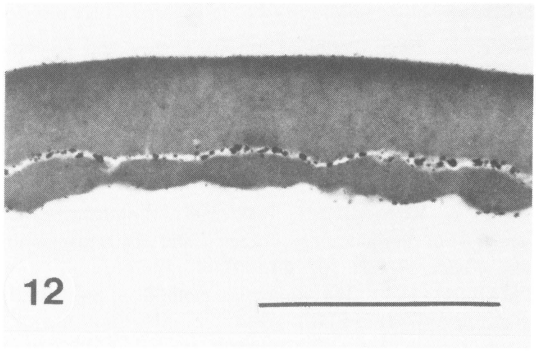
Pollen tetrads and polyads are common in a number of families



Figures 5 – 10 SEM micrographs of tetrads of *Periploca* species. **5.** *P. visciformis* [*Radcliffe-Smith 5390* (K)] rhomboidal tetrad. **6.** *P. visciformis* [*Radcliffe-Smith 5390* (K)] decussate tetrad. **7.** *P. sepium* [*Hancock 37* (K)] linear tetrad. **8.** *P. laevigata* [*Kunkel 9637* (SRGH)] tetrads grouped together. **9.** *P. visciformis* [*Radcliffe-Smith 5390* (K)] pores covered with exine material. **10.** *P. visciformis* [*Radcliffe-Smith 5390* (K)], inner pore edge uneven.







Figures 11 – 13 TEM micrographs of *Periploca* pollen wall showing tectum (T) and granular stratum (G). **11 & 12.** *P. aphylla [Mohammad 2326* (K)]. **13.** *P. acuminata* [*Rahman & Hossain 56* (ABD)]. Scale bars: 1 μm.

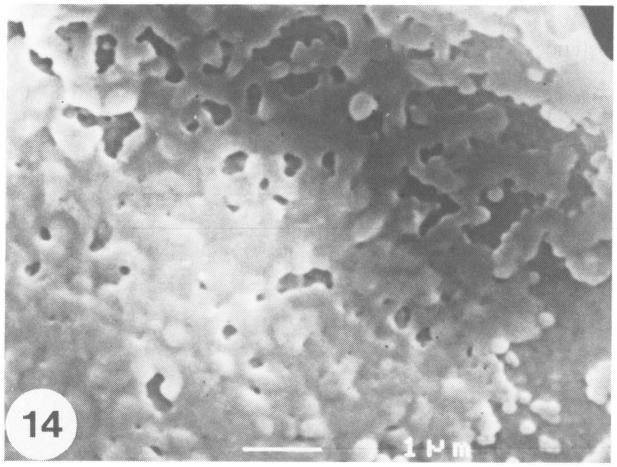


Figure 14 SEM micrograph of *P. visciformis* [*Wood 3168* (K)] broken tetrad, showing inner side of exine.

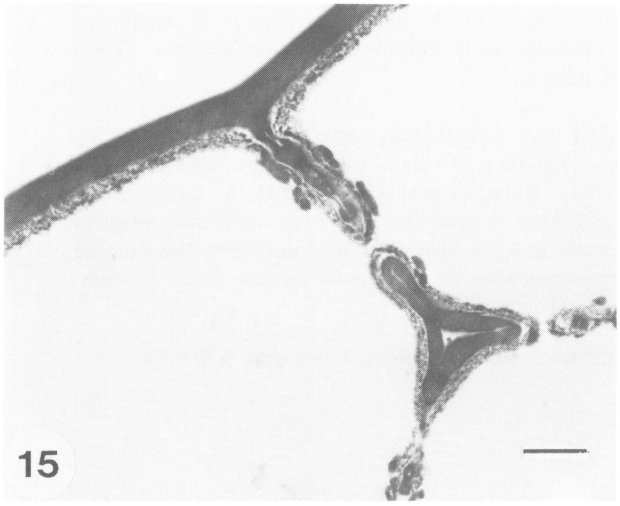


Figure 15 TEM micrograph of section of *P. graeca* [*Chapman 11921* (K)] tetrad, showing the inner walls separating individual grains. Scale bar: 1 μm.

and have been used in systematic treatments to separate genera and species (Oldfield 1959; Skvarla *et al.* 1975; Guinet 1981a,b; Niezgoda *et al.* 1983; Takahashi 1986). In Periplocaceae the pollen morphology is very homogeneous. *Raphionacme* is the one genus which can be distinguished by the 8 – 16 pores per pollen grain (Schill & Jäkel 1978; Lebrun *et al.* 1984; Verhoeven & Venter 1988) as against the 4 – 6 in the other genera. In a few genera, pollen size and arrangement of tetrads may be of taxonomic importance (Verhoeven *et al.* 1989; Verhoeven & Venter 1993). The present study shows that *P. acuminata* can be distinguished from the other *Periploca* species by the size of the rhomboidal tetrads. *P. graeca* and *P. sepium*, both with grains larger than 60 μm, can also be distinguished from the other *Periploca* species. *P. sepium* can be distinguished from *P. graeca* by the presence of linear tetrads. The smallest pollen grains are found in *P. somaliense* and *P. gracilis*.

In all the representatives of the Periplocaceae studied thus far, excepting *Camptocarpus* Decne., *Harpanema* Decne. and *Tanulepis* Balf. f., the exine structure, consisting of a solid stratum (tectum) subtended by a granular stratum, appears to have little variation (Verhoeven *et al.* 1989; Venter *et al.* 1990; Verhoeven & Venter 1993). The *Periploca* species have the same exine structure with little variation. The granular stratum of *P. acuminata*, however, appears more irregular in comparison to the other *Periploca* species. In *Camptocarpus*, *Harpanema* and *Tanulepis* the exine structure is more complete, consisting of a tectum, granular stratum and foot layer (Verhoeven & Venter 1994). The relationship between Periplocaceae and Apocynaceae is illustrated by the presence of an exine structure with a foot layer, and an exine structure consisting of a tectum subtended by a granular stratum also present in the Apocynaceae (Nilsson 1986, 1990).

Acknowledgements

The financial support by the Foundation for Research Development and the University of the Orange Free State is gratefully acknowledged. All the herbaria mentioned are thanked for the kind loan of their specimens.

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A gradient analysis and selection of key ecological species for veld management in a degraded environment near Villa Nora, north-western Transvaal, South Africa

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Received 18 January 1994; revised 5 April 1994

An indirect gradient analysis was carried out on vegetation and environmental data collected in a disturbed area of the Mixed and Arid Sweet Bushveld near Villa Nora, north-western Transvaal. Vegetation ordination axes were correlated with environmental variables deduced to have influenced plant species composition. Soil type proved to be the most significant variable, followed by bush density and canopy cover. Herbaceous species most responsive to the discerned gradients were selected as key ecological species using multiple regression analysis. These species are useful indicators of habitat type and range condition.

'n Indirekte gradiëntanalise is op plantegroei- en omgewingsdata van 'n versteurde gebied in die Gemengde- en Dorre Soet-Bosveld naby Villa Nora, Noord-wes-Transvaal, uitgevoer. Die hoofomgewingsgradiënte wat die samestelling van die kruidlaag beïnvloed, is geïdentifiseer deur plantspesiesamestellingsdata te orden en te korrelleer met omgewingsfaktore. Grondtipe was die belangrikste omgewingsfaktor wat spesiesamestelling beïnvloed het, gevolg deur bosdigtheid en kroonbedekking. Die kruidspesies wat die sensitiefste teenoor die gradiënte gereageer het, is met behulp van meervoudige regressieanalise as ekologiese sleutelspesies geselekteer. Die spesies dien as waardevolle indikators van habitattipe en veldkondisie.

Keywords: Gradient analysis, indicator species, degraded environment, veld management, soil type, bushveld.

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Introduction

Gradient analysis is useful for determining plant species reactions to environmental parameters (Hacker 1983; Walker 1988). For veld management in arid and semi-arid regions it is important to know what plant species are most sensitive to the main environmental parameters affecting veld composition and thus veld condition and grazing capacity (Peel 1990; Beckerling & Trollope 1992). A knowledge of these species can